# NOTES ON SUPERFETATION AND DEFERRED FERTILIZATION AMONG MICE.

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The phenomenon of superfetation, or the occurrence of a second conception in a mammal already pregnant, has been reported and discussed by various writers since the time of Aristotle. The latter[1] refers specifically, in this connection, only to man and the hare. Modern writers[2] have described occasional instances for several animals (man, cat, rat, sheep). On the other hand, this phenomenon appears to have been generally regarded as a biological curiosity, while its very existence has been questioned by some,[3] the facts observed being explained on other grounds. Apparently, it has been very rarely observed in the rat, for Miss King records only two cases among the more than 700 normal broods born in her stock.[4] For mice, I have thus far found no published records of supernumerary broods, though two well-known zoölogists, who have reared varieties of the house mouse in large numbers, assure me that they have encountered cases of this sort. In the absence of exact records, I am unable, however, to report these instances in detail.

In the course of several years' experience in breeding white mice, the present writer has occasionally noted the birth of a second litter, in cases where an earlier litter had been kept with the mother for some time after weaning. This was at first attributed to the precocious sexual development of the earlier male offspring, one of which was held to be the father of the later

[1] See bibliographic references.

[2] Marshall, 1910; King, 1913 (also papers cited by the latter).

[3] Schultze, 1866; Godlewski, 1914.

[4] I do not here include those cases (known as superfecundation), in which members of the same litter, derived from the same period of ovulation, are born one or two days apart. I have myself observed a few cases of this phenomenon, but shall not discuss them here.

brood. In one case of which I have record (Table II., No. 1), this may well have been the true explanation, since the second conception must have occurred when the three males which constituted the first brood were about 42 days old. That male, and even female, white mice may become sexually mature at this age I am certain from independent evidence. I have record of at least one case in which a female, mated to a male of the same brood, became pregnant at an age of about 6 weeks (between 38 and 44 days).

In one instance, however (Table I., no. 6) such an explanation was not applicable, owing to the extreme youth of the first litter, at the time of the second conception. On March 11, 1909, a female gave birth to a brood of two (1 ♂, 1 ♀). On April 8, or 28 days later, a second brood of seven was born. Since the period of gestation of this animal is normally about 20 days,[1] the mice of the first litter were scarcely more than a week old when the second lot began their development. It is needless to point out that a blind and helpless young male of this age could not have played the part of a father. Furthermore, the female had been separated from all other adults of either sex, since the day of the birth of the first brood of young, 28 days previously. Under these circumstances, to be sure, the possibility is not excluded that the second litter resulted from a copulation occurring immediately after the birth of the first. In this event, the only anomaly would be the deferred birth of the later brood of young.

Unfortunately, no further notes on this subject were made during my experiments on white mice. It is my impression that other instances similar to the foregoing were observed, but I find record of only these two cases.

It is the chief object of the present paper to furnish data relating to superfetation and deferred fertilization which have been recorded incidentally during the past two years, in the course of rearing wild mice of the genus *Peromyscus*. Unfortunately, my data are in some cases somewhat equivocal, since the experiments were not made with a view to studying these particular problems. But definite answers can none the less be given to certain questions, even if not to others.

[1] My own observations confirm those of Daniel (1910) on this point.

My stock comprises four geographical races of *Peromyscus maniculatus*, viz., *rubidus*, *sonoriensis*, and two quite distinguishable races within the assemblage generally known as "*gambeli*." In breeding these mice, it is my general practice to place one male with three to five females. Each male is left with the respective group of females for a varying period, which ordinarily does not exceed 20 days. Record is in every case kept of the day when the male is admitted, and of the day when he is removed. Each female, when obviously pregnant, is isolated in a separate cage. The young are ordinarily left with the mother until they are 6 to 8 weeks old. At this time, they are commonly separated according to sex, the males and females being thenceforth kept apart until they are mated, according to the requirements of the work. Occasionally, this separating is not done early enough, however, and matings between brother and sister, or between mother and son, occur. The youngest mice in which I have known fertilization to take place were both 42 days old (possibly a few days younger), the next youngest pair were 55 days old or less. Because of these precocious, and therefore, unexpected conceptions, the exact date of birth of the resulting young cannot always be recorded. They were sometimes several days old when first found. Now it is among very young parents that the phenomena to be discussed seem to be commonest, as will be pointed out presently. For this reason, it happens that in all but two among the eight cases comprised in my first table the father was still present in the cage, and had access to the mother up to the time of the isolation of the latter, when her brood was first discovered. This uncertainty as to the date of the last coition somewhat complicates the interpretation of these cases, though, as will be shown, the evidence, even here, for a deferred fertilization of the ova is not thereby affected.

Before considering the phenomena presented by the tables, it will be well to make inquiry as to the normal period of gestation in *Peromyscus*. Since I have been interested only incidentally in determining this period, I have in no case restricted the mating of the parents to a single observed copulation, as has Daniel (1910), nor have I determined the exact hour of the birth of the brood, as have Long and Mark (1911). I have recorded, how-

ever, the period during which the male had access to the female, and the date of discovery of the brood. During the times when frequent births were expected, the nests were examined daily. Hence a given birth must commonly have occurred between two known observations. It has been my invariable practice to refer the birth to the day when the brood was discovered,[1] except where circumstances were such as to make it probable that the young were born a day or two earlier. In such cases, this probability is indicated in the records.

Since, in a large series of experiments, it is probable that successful insemination would occur in some cases pretty soon after the males were introduced into the cages, it seems likely that the *minimum* interval between the introduction of a male and the birth of a brood represents the actual period of gestation, at least for the individuals in question. This minimum was found to be 22 days. In all but five cases, however, out of a total of 206 broods, for which I have accurate records, the figure was greater than this. As a control, I have determined, for each series, the *maximum* interval between the removal of the male and the discovery of a brood of young. This maximum figure is also a fraction over 22 days. In the single instance recorded, a brood was known to be born as late as some time during the 23d day after the last opportunity for copulation.

From these data, therefore, we know that the period of gestation of *Perŏmyscus* does not, in some cases at least, *exceed* 22 days. We also know that it may be *as much as* 22 days. Accordingly, I have provisionally adopted this figure as representing the normal term for the species which I am engaged in breeding. It is likely, however, that this term is subject to some variation.

Tables I. and II. comprise two different classes of cases. In the former, the interval between the birth of the first and second litters ranges from 13 to 39 days. In all of these cases the youth of the first brood of young, at the time of the second conception, precludes the possibility that a male of the former lot was the father of the second. Even when the interval was as great as 39 days, conception must have occurred when the first lot was

[1] Mice (at least white mice) are said by Long and Mark (1911) to be more commonly born in the early morning than at any other time of day.

# TABLE I.

CASES IN WHICH A MALE OF THE FIRST LITTER COULD NOT HAVE BEEN THE FATHER OF THE SECOND.

| Case No. | Race. | Last Opportunity for Copulation. | Date of Birth of First Litter. | Number When First Counted. | Number Surviving Nearly or Quite to Maturity. | Interval Between First and Second Litters. | Date of Birth of Second Litter. | Number in Second Litter. |
|---|---|---|---|---|---|---|---|---|
| 1 | *gambeli* (LaJ.) | Aug. 12 (or before) | Aug. 12, 1915. | 1 | 1 ♂ | 13 d. (±) | Aug. 25 (±) | 3 |
| 2 | *gambeli* (Berkeley) | July 30 | July 30, 1915 | 2 | none | 26 d. | Aug. 25 | 3 |
| 3 | *gambeli* (LaJ.) | Aug. 11 | Aug. 11, 1915 (or before) | 1 | 1 ♂ | 27 d. (±) | Sept. 7 (or before) | 4 |
| 4 | *gambeli* (LaJ.) | Aug. 11 | Aug. 11, 1915 (or before) | 1 | 1 ♀ | 27 d. (±) | Sept. 7 (or before) | 5 |
| 5 | *rubidus* | May 17 | June 5, 1915. | 2 | 2 ♀ | 28 d. (±) | July 3 (±) | 3 |
| 6 | *albino* (Mus) | March 11 | March 11, 1909. | 2 | 1 ♂, 1 ♀ | 28 d. | Apr. 8 | 7 |
| 7 | *sonoriensis* | Aug. 12 | Aug. 12, 1915 (or before) | 3 | 3 ♂ | 37 d. (or more) | Sept. 18 | 4 |
| 8 | F1 hybrid (*sonoriensis* × *gambeli*) | Aug. 31 | Aug. 28, 1915 (±) | 3 | 2 ♂ | 39 d. (±) | Oct. 6 (±) | 3 |

not over 17 days old, *i. e.*, when the young animals had just opened their eyes. At 4 and 6 days, the young are, of course, blind and helpless. Indeed, in two cases—were further proof needed—it will be noted that the first brood contained no males, while in still another, they had not yet been born.

In cases of the second class (Table II.), the first and second litters were born 63 to 81 days apart, *i. e.*, the second conception occurred when the first brood—which in every case contained a male—was 41 to 59 days old. In these cases, the possibility is by no means excluded that a member of the first litter served as the father of the second. As already stated, there is positive evidence, both in the white mouse and in *Peromyscus*, that fertilization may occur at an age of six weeks. On the other hand, such precocity is quite exceptional, so that this explanation of the cases in Table II. seems hardly more probable than that by which we must explain those in Table I., viz., fertilization by spermatozoa received from the earlier mate. In the absence of definite evidence, however, it would be idle to speculate regarding the relative probability of these two interpretations, and I shall, accordingly, exclude the cases in Table II. from most of the ensuing discussion. Nevertheless, it is worth pointing out—what is not indicated in the table—that the first births recorded in cases 3 and 4 of Table I. are the same as the second births recorded in cases 5 and 9 of Table II. If, therefore, these latter are likewise instances of deferred fertilization, we must assume for these two mothers *the delivery of three consecutive broods, after separation from their mates.* The possibility of such a surprising occurrence surely warrants more carefully controlled experiments in the future.

In the more familiar discussions of superfetation, it appears to be invariably assumed that the later fetuses owe their existence to coition occurring *during the first pregnancy.* This assumption is made by Aristotle, in the passages referred to. Marshall (1910, p. 159) says: "If ovulation takes place during pregnancy, and if, owing to the occurrence of coition the ova become fertilized, the phenomenon of superfoetation may take place—that is to say, foetuses of different ages may be present in the same uterus."

## Table II.

Cases in Which a Male of the First Litter May Have Been the Father of the Second.

| Case No. | Race. | Last Opportunity for Copulation. | Date of Birth of First Litter. | Number When First Counted. | Number Surviving Nearly or Quite to Maturity. | Interval Between First and Second Litters. | Date of Birth of Second Litter. | Number in Second Litter. |
|---|---|---|---|---|---|---|---|---|
| 1 | *albino* (Mus) | ? | Oct. 30, 1908 | 3 | 3 ♂ | 63 d. (±) | Jan. 1 (±) | ? |
| 2 | *sonoriensis* | Aug. 16 | Aug. 23, 1915 | 4 | 1 ♂, 3 ♀ | 71 d. (or less) | Nov. 2 (or before) | 2 |
| 3 | *sonoriensis* | Aug. 16 | Aug. 22, 1915 | 4 | 2 ♂, 2 ♀ | 73 d. | Nov. 3 | 1 |
| 4 | *gambeli* (LaJ.) | Aug. 16 | Aug. 21, 1915 | 3 | 1 ♂ | 74 d. | Nov. 3 | 4 |
| 5 | *gambeli* (LaJ.) | May 17 | May 28, 1915 | 2 | 1 ♂, 1 ♀ | 75 d. (or less) | Aug. 11 (or before) | 1 |
| 6 | *sonoriensis* | ? | June 1, 1914 | 3 | 1 ♂, 1 ♀ | 75 d. | Aug. 15 | 3 |
| 7 | *rubidus* | May 17 | May 24, 1915 | 2 | 1 ♂, 1 ♀ | 79 d. (or less) | Aug. 11 (or before) | 3 |
| 8 | *sonoriensis* | Aug. 16 | Aug. 20, 1915 | 2 | 2 ♂ | 79 d. (or less) | Nov. 11 (or before) | 4 |
| 9 | *gambeli* (LaJ.) | May 17 | May 22, 1915 | 4 | 1 ♂, 1 ♀ | 81 d. (or less) | Aug. 11 (or before) | 1 |

Miss King (1913, p. 385) remarks that "superfœtation . . . is applied to cases in which ovulation, followed by copulation, occurred during pregnancy and led to the simultaneous development in the uterus of two sets of ova belonging to *different* periods of ovulation." In discussing the two instances observed by her in the rat she says: "The most plausible explanation for these cases seems to me to assume that the two ovaries acted independently, ovulation occurring in one ovary some little time before it took place in the other. If copulation followed each ovulation two sets of embryos would develop in the uterus simultaneously, and they would be born at different times, depending on the interval between the two periods of ovulation" (p. 390).

I believe, with the writers quoted, and in opposition to certain others, that these younger fetuses owe their origin to later periods of ovulation, which may even occur during gestation. I cannot see the necessity, however, for assuming an independent action of the two ovaries, as does Miss King. Furthermore, I regard it as highly improbable that some of the cases which I have recorded resulted from a copulation occurring at the time of the later ovulation, whether this last took place during pregnancy or after the birth of the first brood.

*My own observations point, with considerable probability, to two facts:* (1) *to a definite periodicity in ovulation, continuing in some cases throughout pregnancy; and* (2), *with even greater probability, to the retention by the spermatozoa of their fertilizing power for days or even weeks after reception into the uterus or fallopian tubes.*

In support of the first proposition I will point to the rather surprising numerical relations among the figures (Table I.) representing the intervals between the delivery of the two broods by the same mother. These eight numbers are all nearly or quite multiples of 13, viz:

$1 \times 13\ (\pm)$

$2 \times 13$

$2 \times 13,\ (+\ 1?)$

$2 \times 13,\ (+\ 1?)$

$2 \times 13, (+ 2?)$

$2 \times 13, (+ 2)$

$3 \times 13, (- 2?)$

$3 \times 13, (\pm)$

It will be seen that some multiple of a quantity lying between 13 and 14 would fit every case with the exception of one, in which the figure may have been slightly less than 13. Furthermore, let us add Miss King's two cases for the rat. In one of these, the second-born brood was delivered "about 14 days" (but not more than 14 days) after the first. In the other case, the second delivery was, she says, "about 12 days" after the first. It must be mentioned, however, that this "newborn" brood was actually found 13 days after the other.

Here, then, we have altogether 3 instances in which the broods were born about 13 days apart, 5 instances in which the interval was about twice as great, and 2 in which the interval was about 3 times as great. Statistically speaking, the case is not, of course, entirely convincing, and later findings may fail to conform to the scheme here indicated. But the probability seems to be sufficiently high to warrant its provisional acceptance.

Referring to the second table, it will be found that the intervals therein recorded could not all be interpreted as multiples of any one number, though four of them are not far from being multiples of 13. Were one disposed to have recourse to a not uncommon type of argument, he could point out that the normal variability of the single intervals might reasonably be expected to lead to a cumulative divergence in the course of five or six periods. But most of us would be reluctant to draw any conclusions from this second set of figures.

Regarding the existence of a definite periodicity in the ovulation of mice, there appears to be some difference of opinion. Most recent observers seem to agree that ovulation occurs independently of coition in the mouse and rat. Sobotta (1895), Kirkham (1910, 1913), and Long and Mark (1911) hold that it takes place not long after parturition. According to the latter authors the interval between parturition and the ensuing ovula-

tion ranges from $14\frac{1}{2}$ to $28\frac{1}{2}$ hours. Their observations have thrown little light, however, upon the periodicity of ovulation at other times, though they do not seem to believe that this is governed by any great regularity. Sobotta (1895) states that ovulation recurs 21 days after parturition, basing his conclusions upon the examination of several females. He regards as improbable the occurrence of intermediate periods, at intervals smaller than this.

On the other hand, it is stated by Heape (1900) that "the usual length of the diœstrous cycle for rodents is ten to twenty days," that of the rat and mouse (in England) being given as approximately ten days (p. 26). Since it is also stated (Marshall, p. 135) that "in the mouse, the rat, and the guinea-pig, ovulation occurs spontaneously during 'heat,' and generally, if not invariably, during œstrus," it would follow that in these animals, ovulation likewise occurs at intervals of about ten days. This figure approximates much more nearly than Sobotta's to the thirteen-day periods indicated by my observations. Presumably, pregnancy would ordinarily interrupt these periods of ovulation, and initiate a new cycle at its close, though the phenomena of superfetation and deferred fertilization are pretty good evidence that this is not necessarily the case.

If, as seems probable from my data, the second brood of offspring resulted from a later period of ovulation, during or after the first pregnancy, we must suppose that the spermatozoa were retained in an active condition for many days and in some cases even for weeks. Fertilization was deferred until the arrival of viable eggs in the fallopian tubes or the uterus. If we consider the intervals (Table I.) between the last possible opportunity for copulation and the birth of the second litter, we have:[1] no. 1: 13 days ±; no. 2: 26 days; no. 3: 27 days; no. 4: 27 days; no. 5: 47 days (±); no. 6: 28 days; no. 7: 37 days; no. 8: 36 days.

Thus in only a single case (the first) could copulation have occurred as late as 22 days (*i. e.*, the normal period of gestation) before the birth of the second brood. In case no. 5, if we suppose

[1] In all these cases except no. 5 and perhaps no. 1, the first brood was born unexpectedly, and it is likely that the male was still in the cage at the time of delivery.

that the fetuses developed at the normal rate, at least one spermatozoön must have retained its fertilizing power for 25 days or more. In cases 7 and 8, even if we admit the probability here of coition *after* parturition, the spermatozoa must have remained alive for 15 and 14 days respectively.

An alternative hypothesis would be to assume that *gestation* rather than fertilization had been retarded in these cases. Thus Schultze (1866), while not denying the theoretical possibility of superfetation, explains all of the reported cases in man on the basis of either the death or the retardation of the less advanced fetus. This would also seem to be the opinion of Godlewski (1914), who, after pointing out what he believes to be the physiological impossibility of this process, makes the following dogmatic assertion: "Wir müssen demnach annehmen, dass die Eier, welche den Mehrgeburten den Ursprung geben, *gleichzeitig* befruchtet werden" (781). On this assumption, we should have to suppose that, at least in cases 1 and 5, the ova which gave rise to the second brood had been liberated and fertilized simultaneously with those which gave rise to the first. In the remaining cases, on the other hand, they may have been liberated and fertilized after the birth of the first brood.

Now Daniel (1910) has shown for white mice and Miss King (1913) for white rats that parturition may be considerably deferred when the mother is still suckling an earlier brood. This retardation was found, in some cases, to be as much as 10 days for the mouse and 12 days for the rat. Both of these writers assume that fertilization ensues fairly promptly after successful insemination, and that the delay in parturition is due entirely to a prolongation of embryonic development.

If we attempt to apply this interpretation to some of the present examples, we are led into difficulties even greater than those which confront the hypothesis of deferred fertilization. For example, in case 5 (Table I.), the last opportunity for copulation was 19 days before the birth of the first litter, and about 47 days before the birth of the second. Even on the assumption that the fertilization of the second lot of eggs actually took place as late as this last day, the period of gestation was prolonged by about 25 days, *i. e.*, the normal term must have

been more than doubled. Now the first brood consisted of only two individuals, so that any retarding effect due to lactation would have been almost at a minimum. Daniel found that this amounted to only about a day for each young mouse suckled.[1]

If it be contended that the retardation probably resulted from the *gestation* of the first litter rather than their subsequent nursing, it is relevant to point out that this species of *Peromyscus* may give birth to 5, 6, or even 7 young, with little, if any, prolongation of the period of gestation beyond the normal.[2] Again, in cases 7 and 8, the birth of the second brood occurred 37 and 39 days respectively after the first. In both of these cases it is possible that copulation occurred during or shortly after the first pregnancy, since the male was not removed until after the delivery of the first brood. Thus, at the least, we must assume that the second gestation was prolonged more than two weeks, owing to the suckling by the mother of her three earlier young.

To me it seems much more credible that the cases here discussed resulted from the fertilization of recently liberated eggs by spermatozoa which had been received many days previously. I do not think it helps us at all to assume that the term of development, after fertilization, was prolonged to any such extent as we should here have to suppose. Nor do I believe that it is necessary to assume a *second* copulation to account for the later brood, though this possibility is not excluded in my experiments. To refer again to case 5, of my first table, the last opportunity for copulation was 19 days before the birth of the first brood, *i. e.*, only 3 days after the conception which initiated the development of this brood. Is it not as easy to admit the retention of living spermatozoa from this first effective copulation as it is to admit their retention from another copulation occurring only three days later?

At first glance, it is not clear why these cases of deferred fertilization should, in every instance, have followed a previous pregnancy. In other words, why should not this phenomenon

[1] For rats, indeed, Miss King found that retardation was not certain to follow unless more than five young were suckled.

[2] One brood of 6 was born 23 days after the earliest possible fertilization, while one brood of 6 and one of 7 were born 24 days after the earliest possible fertilization.

have appeared in females which had earlier merely undergone insemination, without a normal conception having first ensued? As a matter of fact, I have never found an instance, among all the births recorded, in which a first brood[1] is known to have been born more than 22 days after the last possible opportunity for coition. Why should not the spermatozoa have occasionally been held in reserve for a period of ovulation occurring some time after this last opportunity for copulation? In reply, I can only point out that coition probably occurs only when the female is in a condition of "heat." If, on the advent of the first "heat" period after the introduction of the male, fertilization did not follow insemination, it would, in a large proportion of cases, point to a sterility (temporary, at least) on the part of one or both sexes. As a matter of fact, my records show that the great majority of the females which conceived at all did so during the first half of the sojourn of the male in the cage.[2] As stated above, only one female in the course of my experiments is known to have become pregnant as late as the last possible date of copulation.

To what degree the term *superfetation* is applicable to the cases comprised in my first table is a matter of definition. Case no. 1 (as well as the two cases described by Miss King) would doubtless be covered by the term as ordinarily understood, since one period of gestation, with little doubt, was superimposed upon another. For reasons stated, it does not seem likely, however, that two sets of developing fetuses were simultaneously present in any of the other cases. But in at least one of these instances (no. 5), the sperm which fertilized the second lot of eggs must have been received during or prior to the first pregnancy. Perhaps the term superfetation might conveniently be extended so as to cover such cases as these last. But the word is plainly inapplicable to instances in which the second effective copulation occurred *subsequently* to the delivery of the first brood.

Admitting the last named possibility for most of the cases comprised in my Table I, we none the less find in them instances

[1] *First*, as distinguished from the supernumerary broods here discussed. I do not refer necessarily to the first offspring of a given mother.

[2] This commonly covered 20 days.

of *deferred fertilization*, a phenomenon which has been little recognized among mammals. It is stated by Marshall (1910, p. 136), on the authority of various investigators, that "in certain bats copulation is performed during the autumn, whereas ovulation is postponed until the following spring, the animals in the meantime hibernating, while the spermatozoa are stored up in the uterus." There is no inherent improbability of the occurrence of parallel phenomena in rodents. The presence in the uterus of active spermatozoa long after copulation ought, however, to be directly determined for these animals.

A few additional comments seem worth while before closing these notes. It must be pointed out that, in *Peromyscus*, at least, the phenomena discussed cannot be of very rare occurrence. The seven cases in the first table which relate to deer-mice have been observed in the course of rearing about 250 broods of young. Thus nearly 3 per cent. of the litters born were followed by these deferred or supernumerary broods. Whether or not the small size of these first litters (1 to 3 young) is a matter of significance I cannot conjecture.

Furthermore, it should be stated that most of these supernumerary litters comprised normal, healthy animals, more than 80 per cent. of which survived nearly or quite to maturity. In the great majority, at least, of the cases recorded for man, one, if not both, of the fetuses has been dead or imperfectly developed when born.

Again, it is worthy of remark that in four cases out of eight the parents of these supernumerary broods were both very young mice, which had not yet been separated according to sex, while in two more cases the fathers (though not the mothers) were very young animals. Since the proportion of all my broods born of parents of such an early age is very small, it seems likely that this fact is of some significance.

Finally, the possibility suggests itself that some of the alleged instances of "telegony" which are recorded from time to time, may result from the actual retention of spermatozoa received from an earlier mate. A later copulation with a different partner might happen to coincide with a conception in which the earlier insemination was really the effective one.

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